

MASCULINE DEFICIENCIES IN THE BRITISH VERTIGININÆ.

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INTRODUCTION.

THE researches of Dr. A. E. Boycott and others have revealed the remarkable fact that snails belonging to the genera *Acanthinula* and *Vallonia* very commonly have no male organs, although the individuals are fully developed in other respects and have spermatozoa as well as ova in the hermaphrodite gland.¹ Moreover, when describing the reproductive organs of *Vallonia* three years ago, I briefly mentioned that the same phenomenon occurs in at least one species of *Vertigo*, namely, *V. moulinsiana* (Dupuy). Since then Dr. Boycott has prepared serial sections of several other small snails, chiefly belonging to the Vertigininæ, and has kindly sent them to me for examination. A preliminary study of these very interesting slides has yielded the following results.

BRIEF DESCRIPTIONS OF THE GENITAL ORGANS OF THE SPECIMENS EXAMINED.

Vertigo moulinsiana (Dupuy).

Two specimens collected by Dr. Boycott at Braunton, North Devon, in August, 1919.—In both individuals the male organs are entirely absent, except perhaps for a vestige of the first part of the vas deferens adjacent to the oviduct. The hermaphrodite gland consists of a single cluster of follicles containing both ova and spermatozoa. The hermaphrodite duct is darkly pigmented, as is often the case in the Pupillidæ, and is somewhat swollen near its

¹ Boycott, *Journ. of Conch.*, vol. xv, 1917, p. 175; *Proc. Malac. Soc.*, vol. xii, 1917, p. 221. Steenberg, *Vidensk. Medd. fra Dansk Naturhist. Foren.*, vol. lxix, 1917, p. 6. Watson, *Proc. Malac. Soc.*, vol. xiv, 1920, p. 17.

anterior end, the swollen part functioning as a vesicula seminalis. There is a large albumen gland, as in all the specimens described in this paper. The prostate gland is small, consisting of a very few, short tubules, situated at the inner side of the hinder end of the spermoviduct where it joins the albumen gland. The broad glandular genital duct, which passes forwards from the albumen gland, is divisible into a posterior and an anterior portion, which differ in their histological structure. The posterior part is the larger, and may be termed the spermoviduct; the anterior part may be called the glandular oviduct, and is specially characterized in this species by the fact that its gland-cells contain a granular secretion which stains blue with hæmatoxylin. The last division passes forwards into the non-glandular free oviduct, which unites with the narrow receptacular duct, and is continued to the genital opening as a long vagina of simple structure. The receptaculum seminis, or spermatheca, is situated close to the hinder end of the spermoviduct towards its outer side, not far from the base of the albumen gland; the receptacular duct is therefore very long.

One specimen collected by Dr. Boycott at Cothill, Berkshire, in November, 1921, and nine additional specimens found in the same locality in June, 1923.¹—Five of the latter specimens are without male organs, and closely resemble the examples from Braunton in the structure of their genital ducts. In the remaining individuals from Cothill rather complex male organs are present. The penis is very long, and is somewhat swollen at its hinder extremity; its walls contain a considerable amount of glandular tissue. Into the posterior end of the penis there opens a long epiphallus, which, however, is much narrower than the penis itself and does not contain gland-cells. The slender vas deferens is very long, running forwards near the oviduct and vagina almost to the genital atrium, and then bending round and passing far back to merge into the hinder end of the epiphallus. The narrow penial retractor is inserted at the junction of the epiphallus and vas deferens. The genital atrium is rather short, and the hermaphrodite and female organs agree closely with those of the specimens without male organs.

Vertigo antivertigo (Drap.).

Two specimens collected by Dr. Boycott at Braunton, North Devon, in August, 1919.—Male organs are present in both individuals. The vas deferens is very long, running forwards beside the oviduct and vagina, and then bending round and passing back a considerable distance beyond the hinder end of the penis. It then bends round again and passes forwards to enter the penis at its extremity, this last part of the vas deferens being slightly broader than the rest, and forming an incipient epiphallus. The penis itself is long, and is

¹ Only three of these nine specimens were cut into sections; the rest I dissected in the ordinary manner.

largely lined by glandular cells containing a granular secretion. The flagellum, which Lehmann describes and figures as arising from the base of the penis in this species,¹ seems to be absent.

The genital atrium and the free oviduct are not quite so short as they are in most species of *Vertigo*. The glandular part of the oviduct is larger than in *V. moulinsiana*, and the gland-cells lining it do not contain a deeply staining secretion as in that species, but are less unlike those lining the spermoviduct behind it. The part of the darkly pigmented hermaphrodite duct that serves as a vesicula seminalis is more swollen than in the last species. The hermaphrodite gland, prostate gland, spermoviduct, and vagina are similar to those of *V. moulinsiana*; and so are the receptaculum seminis and its duct, the receptacular duct being very much longer than that shown in Lehmann's figure.

Vertigo substriata (Jeffreys).

Five specimens collected by Mr. Charles Oldham at Dolgelly, Merionethshire, in October, 1922.—The penis is entirely absent in all the specimens. A rather long vas deferens is present near the oviduct, but it appears to end blindly. This species resembles the last in its hermaphrodite gland, spermoviduct, and glandular oviduct; but the non-glandular free oviduct is very short, and the swelling of the hermaphrodite duct that serves as a vesicula seminalis seems to be much smaller.

Vertigo pygmæa (Drap.).

Five specimens collected by Dr. Boycott at Branscombe, South Devon, in August, 1922.—Male organs are present in all the specimens. As in *V. antivertigo*, the vas deferens is remarkably long, with the last part of it slightly broader than the rest, forming an incipient epiphallus. The penis is very long, and its walls contain numerous gland-cells. No appendix or flagellum was found. Lehmann's figure of the male organs of this species² seems to be more accurate than that of Moquin-Tandon,³ the transition from the penis to the epiphallus or vas deferens being abrupt rather than gradual in all the species of *Vertigo* that I have been able to examine.

The genital atrium is very short; the free oviduct is also short, and the glandular part of the oviduct is slightly smaller than in the last two species. The swelling of the hermaphrodite duct that forms the vesicula seminalis is large. The hermaphrodite gland, prostate, spermoviduct, and vagina resemble those of *V. moulinsiana* and *antivertigo*; and, as in these species, the receptaculum seminis is situated on the outer side of the posterior end of the spermoviduct, and therefore has a very long duct, far longer than is shown in the figures of Moquin-Tandon and Lehmann.

¹ *Die lebenden Schnecken u. Muscheln der Umgegend Stettins u. Pommern*, 1873, p. 150, pl. xiv, fig. 52.

² *Op. cit.*, pl. xiv, fig. 53.

³ *Hist. Nat. Moll. France*, Atlas, 1856, pl. xxviii, fig. 42.

Vertigo alpestris, Alder.

Ten specimens collected by Mr. Charles Oldham at Dolgelly, Merionethshire, in September, 1921.—In eight of these specimens no penis can be seen, but as some of this material is not in good condition it is only possible to say with certainty that the penis is entirely absent in the case of four individuals. The first part of the vas deferens is present beside the oviduct, but it ends blindly, sometimes in a slight swelling, at about the level of the anterior end of the receptacular duct or a little below it.

The hermaphrodite duct is darkly pigmented, and is somewhat swollen near its anterior end to serve as a vesicula seminalis. The hermaphrodite gland, the small prostate, and the spermoviduct are similar to those of the preceding forms. The glandular oviduct is rather large, the non-glandular free oviduct is very short, and the vagina is rather long. The receptaculum seminis lies beside the posterior end of the spermoviduct near the albumen gland, and has a very long duct.

In the remaining two specimens of this batch male organs are present. The penis is very long, and is lined by glandular cells containing a granular secretion. The vas deferens enters the penis at its extremity; it is very long and slender, and the last part of it does not appear to be broader than the rest. The genital atrium is very short. The remaining genital organs of these two specimens are similar to those found in the examples without a penis.

One specimen collected in the same locality in October, 1922, is without a penis, and closely resembles the similar specimens collected on the previous occasion, except that the vas deferens is somewhat longer, reaching to the neighbourhood of the genital opening, where it ends blindly in a slight swelling.

The evidence of the genital ducts does not support Boycott's suggestion that this species might prove to be viviparous.¹ On the contrary, it seems very unlikely that any of the species dealt with in this paper are viviparous forms, judging from their structure.

Vertigo pusilla, Müll.

Ten specimens collected by Mr. Charles Oldham at Dolgelly, Merionethshire, in June, 1922, and seven more found in the same locality in October, 1922.—The whole of these seventeen specimens are destitute of a penis; but they possess a vas deferens, which is usually of some length, though it does not lead anywhere. The hermaphrodite gland and its duct, the prostate gland, the spermoviduct, the glandular oviduct, and the free oviduct and vagina are all of the same type as in the last species; but it is noticeable that the secretion in the posterior end of the spermoviduct stains more deeply with hæmatoxylin than that in the anterior part

¹ *Proc. Malac. Soc.*, vol. xiv, 1921, p. 172.

of the same duct, the contrast being somewhat striking, although the structure of the two parts is similar. The receptaculum seminis appears to occupy a similar position in this species to that which it does in the preceding forms.

It will be noticed that the above description does not agree with Lehmann's figure 54, which shows a penis; but there is some doubt as to whether this figure really represents the reproductive organs of *Vertigo pusilla*, which are not described in the text¹; it seems possible that it may portray the genital organs of *V. angustior*, which Lehmann does describe.

Truncatellina britannica, Pilsbry.²

Fifteen specimens collected by Dr. Boycott at Branscombe, South Devon, in August and September, 1922.—Twelve of these snails are without male organs, except that in at least some individuals there may be a vestige of the part of the vas deferens near the oviduct. The hermaphrodite gland, unlike that of the preceding species, is divided into two separate portions. The outer side of both parts is coated with a thick layer of pigment. The hermaphrodite duct is also darkly pigmented, and is only very slightly swollen towards its anterior end. No prostate gland could be found. The broad glandular duct passing forwards from the albumen gland consists of three successive portions, instead of only two, as in the preceding species. These three portions differ widely in their histological structure. The first or posterior portion has a thick compact epithelium of oblong secretory cells, like those commonly found in the wall of the spermoviduct. In the second or middle portion we find large rounded glandular cells, with clear contents. In the third or anterior portion there are smaller ciliated gland-cells, the secretion of which stains a bluish colour with hæmatoxylin. The receptaculum seminis lies against the outer side of the junction of the second and third of these portions; its duct is therefore much shorter than in the species already described. The non-glandular free oviduct is short, and it and the vagina in front of it are of the same simple type found in the preceding forms.

The three other specimens found with the twelve just described are similar, except that they possess male organs. The vas deferens is of moderate length, and leads into the posterior end of a rather small penis without any apparent glandular tissue. No penial appendix was found, such as is described and figured by Lehmann in two other members of this genus.³ It is possible, however, that

¹ Op. cit., pp. 153, 319.

² This form may be a subspecies of *Truncatellina rivierana* (Benson) = *T. strobili* (Gredler), as Pilsbry supposed (*Man. Conch.*, ser. II, vol. xxvi, 1921, p. 77). The name was originally spelt "*brittanica*", but I am informed that this was a printer's error.

³ Op. cit., pp. 140, 148, pl. xiii, fig. 47; pl. xiv, fig. 51.

Lehmann's observations on these very minute species may not be altogether accurate.

Columella edentula (Drap.).

(= *Sphyradium edentulum* (Drap.) of many authors.)

Four specimens collected by Dr. Boycott at Cothill, Berkshire, in November, 1921, and two additional examples found in the same locality in June, 1923.¹—All the specimens have male organs, which consist of a comparatively small penis, without any apparent glandular tissue, and a vas deferens of moderate length, which enters the penis at its extremity. The male organs thus agree with Hanna's description of American specimens,² rather than with the account of Lehmann, who describes and figures two penial appendices in this species.³

The hermaphrodite gland appears to form a single cluster of follicles. The hermaphrodite duct is darkly pigmented, and is swollen near the albumen gland to serve as vesicula seminalis. An extremely small prostate gland seems to be present on the inner side of the posterior end of the spermoviduct, that is to say, in the usual position of the prostate in the Pupillidæ. The spermoviduct and the glandular oviduct in front of it are both rather large, and of the same general character as in *Vertigo antivertigo* and *V. substriata*; but where they join there is a part having a slightly different histological structure, which may possibly correspond to the more distinct middle portion of the glandular genital duct of the last species. The non-glandular part of the oviduct is short; the vagina is longer, but the genital atrium is very short. The receptaculum seminis is situated near the junction of the spermoviduct and the glandular oviduct, *i.e.* about half-way up the glandular part of the genital duct, and is nearer the inner than the outer side. The receptacular duct is therefore of moderate length.

These specimens differ from Hanna's description in that the hermaphrodite duct is slightly convoluted towards its anterior end, the glandular wall of the spermoviduct is folded internally, and the genital atrium, though very short, is not entirely absent. These apparent differences, however, may be chiefly due to differences in the methods of observation; they need not be held to prove that the form examined by Hanna is specifically distinct from that found in England, especially as Sterki has stated that "the American form is absolutely identical with the palæarctic".⁴

THE PRESENCE AND ABSENCE OF MALE ORGANS IN THESE SPECIMENS.

The following table summarizes the facts respecting the presence and absence of male organs in the specimens described above:—

¹ These two specimens were not cut into sections like the others, but I examined their male organs by ordinary dissection.

² *Proc. U.S. Nat. Mus.*, vol. xli, 1912, p. 375.

³ *Op. cit.*, p. 143, pl. xiv, fig. 49.

⁴ *Nautilus*, vol. x, 1896, p. 76.

	Number of individuals	
	With penis	Without penis
<i>V. moulinsiana</i> , Braunton	0	2
„ Cothill	5	5
<i>V. antivertigo</i> , Braunton	2	0
<i>V. substriata</i> , Dolgelly	0	5
<i>V. pygmæa</i> , Branscombe	5	0
<i>V. alpestris</i> , Dolgelly	2	5 (at least)
<i>V. pusilla</i> , Dolgelly	0	17
<i>T. britannica</i> , Branscombe	3	12
<i>C. edentula</i> , Cothill	6	0
Totals	23	46

It will be noticed that in three of these species all the specimens examined possess a penis; in two species none of them do; while in three species some of the individuals have a penis but the majority are without this organ. No intermediate specimens occurred in which the penis was only partly developed; it seems to be always either present or entirely absent. In those animals which lack a penis the other organs are fully developed, and spermatozoa are present in the hermaphrodite gland and duct. Moreover, in at least some of these species, as in the case of *Acanthinula aculeata* and *Vallonia costata*, specimens with and without a penis may be found together at the same time and in the same locality.

These facts show that the frequent absence of the male organs in this family of snails can scarcely be due to the immaturity or senility of many of the specimens, or to any influence of the environment; it would seem more probably to be a mutation caused by some hereditary factor.¹ But as this mutation is so common among these snails, it is probable that the absence of a penis does not seriously interfere with the animal's reproductive powers in the case of these minute species. Possibly the spermatozoa pass straight down the oviduct and vagina, which are no broader than the vas deferens and epiphallus of a large snail; and in copulation the very short distance that they have to travel may render a special intromittent organ unnecessary. On the other hand, it is quite possible that self-fertilization, which evidently occurs occasionally in some of the larger snails and slugs, may be the normal method of reproduction in these genera. The chances of successful copulation would not only be reduced by the limited locomotory powers of such small snails, as

¹ The ten species in which this phenomenon is now known to occur belong to four different genera; nevertheless, they are all orthurethrous forms not distantly related to one another. Collinge has described single abnormal specimens of *Arion intermedius* Normand and *Helix aspersa* Müll. with no male organs; but these are extremely rare abnormalities, and in them the receptaculum seminis is said to be absent, as well as the male ducts (*Journ. of Anat. and Physiol.*, vol. xxvii, 1893, pp. 237, 238).

Boycott has pointed out,¹ but also by the fact that, while spermatozoa are present in considerable numbers in the hermaphrodite gland in these forms, irrespective of whether the animal has a penis or not, they do not occur in the enormous quantities that one commonly finds in the genital glands of other snails. This is probably due to the small size of the gland, which does not leave room for a very large number, most of the space being occupied by the ova. In this connexion it is interesting to note that, of the species examined, the two in which the swelling of the hermaphrodite duct that serves as a vesicula seminalis is largest, namely, *V. antivertigo* and *V. pygmæa*, are the only species of *Vertigo* in which all the specimens examined possess a penis.

Dr. Boycott has also pointed out that it would be specially advantageous to very small snails to dispense with any superfluous organs, in order to leave greater room for the more essential structures.² The complex organs possessed by a snail are in most cases built up of a very large number of cells, and the size of the individual cells cannot be reduced indefinitely³; therefore a stage must be reached when some of the organs can scarcely become any smaller. Accordingly, in a minute snail the organs are likely to become unduly crowded, and it will then be an advantage to dispense with any that are unnecessary in order to leave room for the efficient working of those that are more essential. If the male organs can be dispensed with, more room will be left for the adjacent buccal mass and central nervous system, very complex and necessary structures.⁴ And there will also be more room for the passage of the eggs down the female ducts; for the eggs cannot be reduced below a certain size if they are to contain a sufficient store of food material to carry the young snail through the whole of its development, until it is hatched in a form in which it is able to feed itself.

To this argument it might perhaps be objected that some of the species with male organs, *Vertigo pygmæa* for example, are even smaller than some of those that are frequently without a penis.

¹ *Proc. Malac. Soc.*, vol. xii, 1917, p. 225. It may be observed that the three species in which no specimens without male organs have yet been found are those that are the most widely distributed throughout the British Isles. On the other hand, some of the species that seem to be usually without male organs are sometimes found in considerable numbers in the small areas in which they occur; and in such instances it may be doubted whether the chances of two individuals meeting each other are less than in the case of a few of the larger, but less gregarious, forms belonging to other groups which are not known ever to lack a penis. Moreover, the species of *Vallonia*, which seldom possess male organs, are by no means rare snails.

² *Journ. of Conch.*, vol. xv, 1917, p. 177.

³ See D'Arcy Wentworth Thompson, *On Growth and Form*, 1917, pp. 34-8, on the factors that limit reduction in the size of cells.

⁴ It is even conceivable that the pressure of these organs at an early and critical stage in the development of the genital ducts might possibly be a direct cause of the suppression of the male organs.

This objection, however, fails to take into consideration the fact that in these relatively larger forms, such as *Acanthinula aculeata*, the male organs, when present, are specially complicated and therefore presumably occupy more space.

THE EVIDENCE OF THE GENITAL ORGANS IN CONNEXION WITH THE CLASSIFICATION OF THE BRITISH VERTIGININÆ.

A detailed study of the entire anatomy of a larger number of specimens will be necessary before we can form an adequate judgment of the mutual affinities of these small species. Nevertheless, it is worth noticing that if the species dealt with in this paper were to be classified according to their genital organs alone, the result would be somewhat as follows:—

(1) Penis (when present) long, containing glandular tissue; vas deferens very long; receptacular duct also very long.—*Vertigo moulinsiana* (Dupuy), *V. antivertigo* (Drap.), *V. pygmaea* (Drap.), *V. alpestris*, Alder, and almost certainly *V. substriata* (Jeffer.) and *V. pusilla*, Müll., although in the last two species the form of the penis, if that organ ever occurs, is not yet known.

(2) Penis (when present) rather small, without glandular tissue; vas deferens not exceptionally long; receptacular duct of moderate length.

(a) Glandular part of genital duct composed of three portions differing widely in structure; hermaphrodite gland divided into two parts.—*Truncatellina britannica*, Pilsbry.

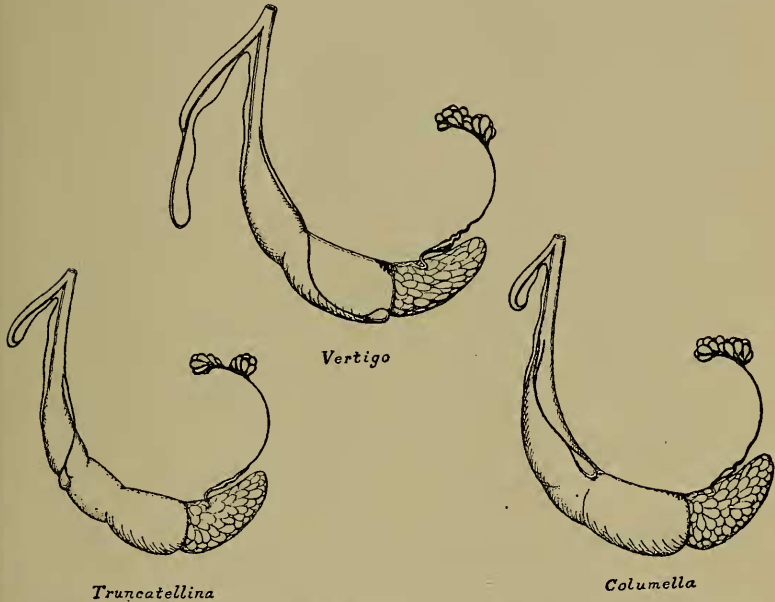
(b) Glandular part of genital duct composed of two main portions differing slightly in structure; hermaphrodite gland not divided into two parts.—*Columella edentula* (Drap.).

It will be seen that this classification agrees remarkably well with one founded solely on the characters of the shell. If, however, the radula were also to be taken into consideration, *V. moulinsiana* would probably have to be placed slightly apart from the other British species of *Vertigo*, for the radula of this species is peculiar in that the lateral and marginal teeth are all approximately Π -shaped, and scarcely differ from one another.¹

The reproductive system of *Truncatellina britannica* differs in several respects from that found in the other species examined, as may be seen from the description given above (on p. 274). It is thus evident that this species is rightly placed in a distinct genus. Its radula may be described as intermediate in character between the type found in *Vertigo pygmaea* and its allies, and that found in the genus *Columella*; but it more nearly resembles the former type than the latter. In this minute species there are not more than eleven teeth on each side of the central in each transverse row.

¹ See Tomlin and Bowell, *Journ. of Conch.*, vol. xii, 1909, pp. 215, 298, pl. v.

The reproductive organs of *Columella edentula* in some respects resemble those of the last species, while in other features they are more like those of the genus *Vertigo*, though they differ from both in the position of the receptaculum seminis. There can be no doubt, however, that Hanna was right when he stated that this snail is far more nearly related to *Vertigo* than to *Punctum*,¹ a very different genus, with a sigmurethrous excretory system and deep peripodial grooves. Even in its jaw it seems to me that *Columella edentula* more closely resembles *Vertigo* than *Punctum*, although the character of this organ has formed one of the chief grounds for regarding this animal as related to the latter genus. The multiple jaw of *Punctum*



Diagrammatic figures illustrating some of the differences in the reproductive organs which appear to separate the type found in most of the British species of *Vertigo* that possess male organs from the types occurring in *Truncatellina* (when male organs are present) and in *Columella*.

and *Laoma* is a very distinctive organ of peculiar structure, whereas the jaw of *Columella edentula* seems only to differ from that of *Vertigo* in that the oblong plates of which it is composed are less closely united with one another. For in *C. edentula* the plates of the jaw do not seem to be entirely disconnected, and in the genus *Vertigo* the jaw often has the appearance of being built up of a number of plates which are joined to one another but have not become entirely fused together. The type of teeth found in the radula of *Columella*

¹ *Proc. U.S. Nat. Mus.*, vol. xli, 1912, p. 371.

might easily have been derived from that occurring in *Truncatellina*; and the resemblance of the radula of this genus to the type found in *Punctum* should probably be regarded as due to convergence. The cusps of the teeth in two English specimens of *Columella edentula* were not observed to have the blackish colour that Dall states he found in some American examples.¹

SUMMARY.

A study of Dr. Boycott's preparations shows that the penis is very commonly entirely absent in *Vertigo pusilla*, Müll., *V. substriata* (Jeffer.), *V. alpestris*, Alder, *V. moulinsiana* (Dupuy), and *Truncatellina britannica*, Pilsbry, although it has been found in a few specimens of the last three species, as well as in *Vertigo pygmæa* (Drap.), *V. antivertigo* (Drap.), and *Columella edentula* (Drap.). The specimens without a penis are fully developed in other respects, with spermatozoa as well as ova in the hermaphrodite gland; the part of the vas deferens near the oviduct is usually present, but it ends blindly.

A classification of the British Vertigininæ based on the genital organs agrees well with that founded on the shell, although the radula of *V. moulinsiana* suggests that this species stands slightly apart from the other members of the genus *Vertigo*. The reproductive organs of *Truncatellina* differ in some respects from those of *Vertigo*, and the male organs (when present) resemble those of the genus *Columella*. No evidence has been found in support of Lehmann's statements that flagella occur in various species belonging to these three genera; on the other hand, Hanna's views about the simplicity of the male organs of *Columella edentula*, and the affinities of this animal with *Vertigo* rather than *Punctum*, are confirmed.

THE PRESENCE OF A SUB-CEREBRAL COMMISSURE IN THE ORTHURETHRA.

By HUGH WATSON, M.A.

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THE cerebral nerve-ganglia might be termed the brainiest part of a mollusk, and the commissures that unite these two ganglia are structures of considerable importance. For if the chief nerve-centres on the right and left sides were not directly connected with each other, it is difficult to perceive how an animal could efficiently regulate its actions to achieve definite ends. To be double-minded is to be unstable in all one's ways.

It is well known that in the most primitive order of Gastropods, the Aspidobranchia, the cerebral ganglia are directly connected by two commissures, one passing above the buccal mass and the other

¹ *Proc. U.S. Nat. Mus.*, vol. xli, 1912, p. 372.